

A FOSSIL INSECT WING BELONGING TO THE NEW
ORDER PARAMECOPTERA, ANCESTRAL TO THE
TRICHOPTERA AND LEPIDOPTERA, FROM THE
UPPER COAL-MEASURES OF NEWCASTLE, N.S.W.

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(Plates xii.-xiii., and eight Text-figures).

The working out of Mr. John Mitchell's Collection of Fossil Insects from the Upper Coal-Measures of Newcastle, New South Wales(4), proved the existence of Holometabolous Insects in Palæozoic times, the genus *Permochorista* from Belmont being an undoubted Mecopteron, closely allied to, and almost certainly directly ancestral to, the genus *Teniochorista* found in Australia at the present day. That being so, the great importance of these fossils to science became at once evident; since further discoveries would almost certainly throw new light upon the all-important problem of the origin of the Holometabola. I therefore arranged with Mr. Mitchell to visit the Belmont Beds, in order to see for myself the place where he had found the fossils.

In my previous paper (4, p.723), I gave a figure of a vertical section through the Upper Coal-Measures, showing the exact position of the Belmont Beds within them. As there stated, they lie about 600 feet below the top of the Upper Coal-Measures, and may therefore be regarded as of Upper Permian age. I can now add a few impressions of the Beds themselves as I saw them.

Some two miles back along the Newcastle Road from Belmont, there has been quarried out from the top of a low, wooded hill a quantity of hard, cherty shale. This was made use of for a time for mending the road, but was found unsuitable, so that the quarry was soon abandoned. The band of cherty shale is nowhere more than a yard thick, and is only uncovered in an irregular

manner for some fifty yards or more; so that the amount of material at present available for fossil-hunting is very small. Mr. Mitchell, a friend, and myself worked through a large quantity of it in one day, the only result being the discovery of another wing of *Permofulgor* in excellent condition; this fell to Mr. Mitchell's hammer. The rock splits sometimes with a plane, and sometimes with a conchoidal fracture. The plant-remains consist chiefly of *Glossopteris* in an excellent state of preservation. Occasional specimens of the small Crustacean *Leaia mitchelli* Eth., are also found. The fronds of *Glossopteris* are never closely crowded together; usually not more than one or two will be found within a large hand-specimen of rock. Thus the conditions are ideal for the preservation of insect wings; for these, when they occur, likewise lie quite free from plant-remains, and the impressions that they have made on the hard rock are almost as good as one could hope for. Against this it has to be borne in mind that insect-remains are very rare indeed at Belmont, and one is indeed fortunate if, as the result of a hard day's work, a single wing falls to one's lot.

My visit to Belmont took place in June, 1918. While staying with Mr. Mitchell at Waratah, he very kindly looked over some old material from Belmont and Glenlee, with the result that several insect wings were found and handed to me to describe. These will be dealt with in a separate paper later on.

Mr. Mitchell again visited the Belmont Beds in February of this year. As a result of two days' work, a single wing was found, very beautifully preserved, and almost perfect. This was sent at once to me, Mr. Mitchell being unable to determine it, and thinking that it might turn out to be something good. It is this wing that forms the subject of this paper. It is indeed a wonderful discovery, and one upon which Mr. Mitchell is greatly to be congratulated. For it solves, as it were at a single stroke, the long-vexed question of the origin of the Trichoptera and Lepidoptera; while at the same time throwing a flood of light upon the probable origins of the other Panorpoïd Orders.

As this wing is of such great scientific interest, it was decided that it should be dealt with in a separate paper, while the

remaining Belmont fossils might reasonably be postponed to a later date, although they were discovered earlier than the one here dealt with.

The characters of the wing are such that it cannot be placed in any known Order, either fossil or recent. It is undoubtedly allied to the Mecoptera and Protomecoptera, on the one hand, and to the Trichoptera and Lepidoptera on the other. Its relationships with the first two Orders mentioned are *collateral*, as will be clearly seen when we come to compare it with *Permochorista* from the same Beds. With the Trichoptera and Lepidoptera, on the other hand, its relationships are definitely *ancestral*; a comparison of the fossil wing with *Rhyacophila* and *Micropteryx* will show quite clearly that both these types can be directly derived from the fossil by reduction, without a single discordant character. That being so, we are now able to state definitely, not only that the Mecoptera (and, of course, the Triassic Protomecoptera also, though not yet found in Palæozoic strata) were in existence in Upper Permian times, but that the Trichoptera and Lepidoptera were not then differentiated, being represented by a common ancestral type closely allied to the Mecoptera, such as we find in this fossil.

The above relationships have suggested to me the name Paramecoptera for the new Order. Not only does this name indicate the collateral evolution of the new type alongside the Mecoptera, but it also allows future entomologists, should they so desire, to merge the new Order into the Mecoptera, together with the Protomecoptera; so that a single Order Mecoptera, with its characters defined on a wider basis, may one day be made to include the three Suborders Paramecoptera (Permian), Protomecoptera (Triassic), and Eumecoptera (fossil and recent), these last being the true Mecoptera, or Scorpion-flies, as at present understood. For the present, however, the difficult task of the Phylogenist in these groups can only be undertaken with clearness if these new types, about which we know so little, are given distinct ordinal rank, thus marking out clearly, and without any ambiguity, the venational characters of each separate type within the complex of the Panorpid Orders. That being so, I propose to

define at once the new Order, and to describe the fossil wing placed within it. A full discussion of its relationships will follow this description.

Order **PARAMECOPTERA**, ordo nova.

Fossil insects belonging to the Subclass Panorpoidea, and having the same general venational scheme as those of the older existing types within the Trichoptera and Lepidoptera, but with a larger number of branches to both Rs and M. The *posterior arculus* well developed, its connection with the cubitus being of the same nature as in the *Rhyacophilidae* and the Homoneurous Lepidoptera. No separate costal vein. Rs dichotomously branched, with at least seven separate branches on the wing-margin. M dichotomously branched, with five separate branches on the wing-margin. Cu three-branched (as in Megaloptera, Trichoptera, and Lepidoptera). Cu₁ having an apical fork, while Cu₂ is a weak, concave, simple vein. Anal veins simple. System of cross-veins the same as that of the older Trichoptera, with a few additions; no development of regularly spaced cross-veins at intervals, as in the true Mecoptera.

Family BELMONTIIDÆ, fam.nov.

Moderate-sized insects with fairly long and narrow wings. Costal space narrow, with humeral cross-vein present. Both radial and median cells closed. The dichotomy of R₄₊₅ into R₄ and R₅ takes place very close to the first dichotomy of Rs into R₂₊₃ and R₄₊₅. Median fork at about two-fifths from base of wing; three cross-veins between Rs and M₁₊₂ or M₁, also a short basal cross-vein from R to M, just distad from origin of posterior arculus.

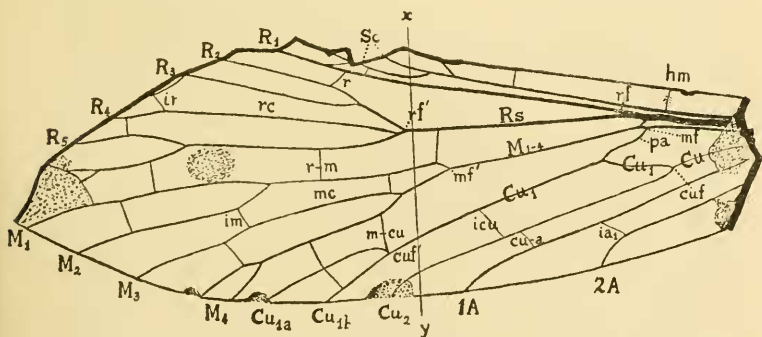
Genus BELMONTIA, n.g.

(Plates xii.-xiii.; Text-figs.1-3).

Forewing.—Subcosta forked distally, ending up at about half the wing-length; costal space with two extra veinlets between the humeral cross-vein and Sc₁. R₁ connected with Rs by a single cross-vein below end of Sc₂. Radial cell irregular, elongate, six-sided, the two most distal sides being the basal portion of R_{3b}.

and the inter-radial cross-vein respectively. R_3 and R_5 both forked, the posterior portion of R_5 (*i.e.*, R_{5b}) again forked distally. R_4 connected with R_{5a} by a single cross-vein. Median cell narrow, elongated, six-sided, closed distally by the inter-median cross-vein, and crossed internally by an extra cross-vein at its basal third. Apical fork between M_1 and M_2 crossed by an extra cross-vein; the same is true of the apical fork between M_3 and M_4 , but the cross-vein descends upon the upper branch of a small fork made by the bifurcation of M_4 into two veins distally. Cu_1 forks at a level about half-way along the wing, the fork being supported by a cross-vein from M_4 directly upon it. Apical fork between Cu_{1a} and Cu_{1b} crossed by an extra cross-vein, which is continued above to M_4 . Single cross-veins, as usual, connect the branches of Cu and the anal veins. (Third anal vein and jugal lobe missing in the fossil, also a portion of the apical area of the wing).

Genotype, *Belmontia mitchelli*, n.g. et sp. (Upper Coal-Measures of Newcastle, N.S.W.).



Text-fig. 1.

Belmontia mitchelli, n.g. et sp., forewing ($\times 6$). Upper Permian of Belmont, N.S.W. *xy* indicates the line along which the rock was broken in two. For rest of lettering, see Text-fig. 2, p. 238.

BELMONTIA MITCHELLI, n.sp. (Plates xii.-xiii.; Text-figs.1-3).

This species is represented by a single forewing, as shown in Plate xii. and Text-fig. 1. The extreme base is covered over by a small piece of rock which, owing to its conchoidal fracture,

cannot be removed without serious risk of damaging the specimen. The rock has also broken away obliquely at the opposite end of the wing, so that an apical portion carrying the distal ends of all the branches of R and Rs is missing. Besides this, Mr. Mitchell informs me that, in trying to clear the base of the wing, he unfortunately broke the rock in two, transversely across the middle of the wing; the two parts have, however, been carefully glued together, so that the break is barely noticeable. This break is indicated by the line *xy* in Text-fig.1.

Total length of preserved portion of wing, 16 mm.; *greatest breadth*, 5.5 mm. Approximate total length of complete wing, 20 mm. The impression is that of a forewing, and is the *mould*, not the cast; this is proved by the fact that the strongly convex veins R and Cu₁ appear as deep grooves instead of raised ridges. Consequently, although the apex of the wing lies to the left in the fossil, the wing itself was the *right* forewing.

The venational characters have all been included in the generic definition given above. Besides these, it may be added that the main veins mostly show, under a good oblique light, the bases of macrotrichia; but these cannot be seen on the cross-veins. The membrane was evidently very thin, as usual also in Trichoptera and many Lepidoptera, and shows the peculiar oblique rucking and stretching usual in fossils of these Orders and also in the Diptera. A very careful examination reveals slight traces of an archedictyon in places, apparently with some rather small macrotrichia upon it; but these indications are scarcely more than would be seen if the meshwork were in the last stage of aphantoneurism.

In Text-fig.1, the base of the wing is represented as cut off in the conventional manner; but as a matter of fact the wing disappears along the basal break *underneath* a portion of rock some 1½ mm. higher than the level of the wing itself.

Type in Mr. John Mitchell's Collection. *Label*, "No. 40, Wing. Loc. Belmont. Coll. J. Mitchell," on back.

Locality, Belmont Beds, Upper Coal-Measures, near Newcastle, N.S.W. (Upper Permian).

Restoration of the Fossil Wing. (Text-fig.2).

It will be seen at once, from Text-fig.1, that practically all the essential parts of this wing have been preserved. This makes the task of restoring it an easy one. Most of the wings of Holometabolous insects so far found have been incomplete, or obscure, as regards the venation of the basal part of the wing. Hence it is a particular piece of good fortune that the posterior arculus and its surroundings have been perfectly preserved in this fossil. The only vein missing is the short 3A, with the jugal lobe lying basad from it. In restoring this part, I have assumed a simple 3A, connected with 2A by a single cross-vein, in the same way that 2A is itself connected with 1A. The jugal lobe has been restored on the primitive plan, as in *Chorista*, and I have omitted the jugal bristles, since these are not known to be present outside the true Mecoptera. Mr. Mitchell hopes later on to make another attempt to remove the rock covering this part of the wing; but the risks attaching to such an attempt are so great, that it is necessary to describe the fossil as it stands first of all, in case of damage later on.

In restoring the apical part of the wing, I have introduced no more forkings to the branches of Rs than can already be seen in the fossil, i.e., each vein has just been produced to the apical margin. The spacings between them show that this is almost certainly correct. In the case of R_1 , however, there is a wide space to be filled up between Sc_2 and R_2 , so that I have introduced a distal forking to this vein. The apex itself I have made slightly pointed, as this type of wing is much more representative of the older types of Trichoptera and Lepidoptera than is the rounded wing, which predominates in the true Mecoptera. Whether there were any extra apical cross-veins it is impossible to say; but I think it very unlikely. The restored right forewing is shown complete in Text-fig.2.

Affinities of the Fossil. (Text-figs.3-8).

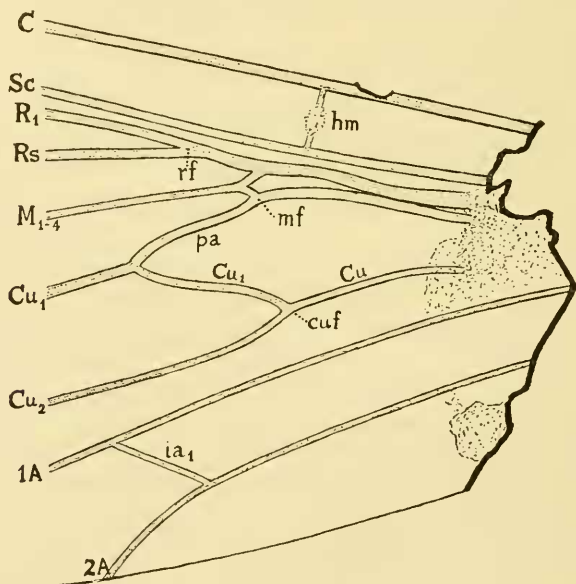
In his recent work upon the Wings of Insects(1), Professor Comstock rightly insists upon the importance of the presence of the *posterior arculus* in the forewings of the more archaic Tri-

choptera and in the *Micropterygidae*. This character is also to be found in the *Hepialidae*. In studying the pupal wings of Lepidoptera, the same condition can be seen to exist throughout the Order, the bend of Cu_1 being distinctly shown, with the posterior arculus, usually devoid of a trachea, above it. In the imagines of the more advanced types of both Trichoptera and Lepidoptera, the posterior arculus cannot usually be recognised, as it becomes obliterated by further specialisation in this region of the wing.

In naming this formation the *posterior arculus*, Comstock assumes that it is the homologue of the posterior portion of the complete arculus found in the Odonata, *i.e.*, that it is formed from a cross-vein descending from M to Cu_1 , which later on becomes specialised as a strong oblique connection carrying Cu_1 back basally to join M. Another possibility is that the posterior arculus is really the remnant of the posterior branch of the first dichotomy of M; in other words, that it is the homologue of M_4 in the Odonata. If this be so, then this branch of M must very early have united with Cu_1 not far from its origin, in the same manner that M_4 united with Cu_{1a} later on in the Lepidoptera, and M_{3+4} with Cu_1 in the Planipennia. If this latter supposition be true, then the correspondence between the media in Zygopterous Odonata and in the Trichoptera and Lepidoptera is exact, both having five branches similarly placed, and the primitive dichotomic branching being still preserved in the *Synlestinae*. Only the notation is different, the branches in the Zygoptera being called M_1 , M_2 , M_s , M_3 , and M_4 respectively; whereas, in the other Orders, they are M_1 , M_2 , M_3 , M_4 , and M_5 , the latter being the posterior arculus.

The evidence as to whether the posterior arculus is really a branch of M, or only a specialised cross-vein, has hitherto been inconclusive. On the one hand, we find that, in the freshly turned pupæ of *Hepialidae*, *Cossidae*, and other archaic Lepidoptera, the posterior arculus is marked by a very distinct pale band, not traversed by any trachea; on the other, a distinct trachea can generally be seen to have grown out into it from near the base of M, in pupæ of more advanced age. This trachea

sometimes increases in length, and may be seen traversing the cubitus in the imaginal wing. Again, in most species of *Rhyacophila* (rightly regarded as being one of the most archaic of existing Trichopterous genera), the posterior arcus is well developed; but other species exist in which it is reduced to a short cross-vein, or even obliterated by complete fusion of M with Cu_1 . Which of these conditions is the most archaic?



Text-fig.3.

Belmontia mitchelli, n.g. et sp., to show the preserved portion of base of forewing, enlarged, ($\times 17$). Upper Permian of Belmont, N.S.W. For lettering, see Text-fig.2, p.238.

In our new fossil, as can be seen from Plate xiii. and Text-fig. 3, the posterior arcus appears as a very strongly formed convex vein. If it is a cross-vein, then it is very different from any other cross-vein in the wing, since all the others are much more weakly chitinised. Now I have already shown, in a previous paper(5), that, in all archaic Panorpoid types, macrotrichia are present upon the main veins and their branches, but are absent

from the true cross-veins. We have, then, a test in this fossil: does the posterior arcus carry macrotrichia or not? The basal two-fifths of this vein are unfortunately not very well preserved, but the remainder is in excellent preservation, and *the bases of at least two macrotrichia can be seen upon it*. One of these is very beautifully preserved, and is indicated by the large arrow placed just below it in Plate xiii., fig.3. The other can just be made out, a little higher up, in the same Plate, but is not very distinct. Similar bases of macrotrichia can be seen upon the other main veins of the wing; a particularly good one can be picked up on Cu_1 by following the main stem of the same arrow in Plate xiii., fig.3, backwards. These bases are more abundant and better preserved in the apical part of the wing, where the veins are, on the whole, more clearly defined.

It seems evident, therefore, that the posterior arcus must be rightly considered as having been originally M_5 , and the exact homologue of M_4 in the Zygopterous Odonata. If so, then the vein that we now call Cu_1 may well be actually $M_5 + Cu_1$, and its distal forkings may be due to incomplete fusion of the two veins M_5 and Cu distally, Cu_{1a} being really the distal portion of M_5 , and Cu_{1b} the distal portion of Cu_1 . It should be noted that the term *posterior arcus* is a misnomer, if this be really the case; for it is the *anterior* part of the arcus in Odonata that is formed from M , the posterior part being a cross-vein. Also the point of origin of M_5 should be rightly designated the *primary median fork* (mf'), while the point at which M_{1-4} divides into M_{1+2} and M_{3+4} , hitherto designated mf' (sometimes called the *thyridium*), must be regarded as the *secondary median fork* (mf'').

I would suggest that the term posterior arcus should be no longer used for the vein in question, and that it be simply designated the *arcus*, with the notation *arc* or M_5 .

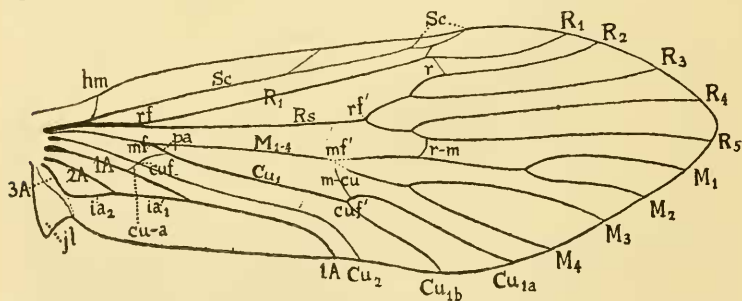
An examination of the arcus in the Caddis-fly *Rhyacophila dorsalis* Curtis, reveals the fact that, in this insect also, this vein carries macrotrichia. This is in agreement with the evidence from the fossil, so that there can really be little doubt that we are dealing with a true branch of the media.

But, whatever view we may take as regards the true nature of

the vein forming the arculus, we have to face the fact that it is present in our new fossil, and more strongly formed than in any other known type within the Panorpid Orders, either fossil or recent. Now the arculus, in the form in which we find it in this fossil, is typical of the oldest existing Trichoptera and Lepidoptera. It does not occur in the Mecoptera, with the single exception of the Triassic fossil *Stereochoristu*(7). In the Diptera, the arculus is present, but of different form from that in the fossil; in the Megaloptera and Planipennia, it has not yet been shown to occur at all. The conclusion, then, is obvious, that *our fossil must be closely related to the archaic types of existing Trichoptera and Lepidoptera.*

(i.) *Affinity with the Trichoptera.*

We may take the forewing of *Rhyacophila dorsalis* Curtis, (Text-fig.4) as a good example of the wing of an archaic Caddis-fly. Comparing this closely with the wing of *Belmontia*, it will readily be seen that the wing of the Caddis-fly can be directly derived from that of the fossil, simply by reduction of certain parts.



Text-fig.4.

Rhyacophila dorsalis Curtis, forewing, ($\times 8$). Scotland, recent; Order Trichoptera. For lettering, see Text-fig.2, p.238.

The resemblance between the subcostal veins of the two wings is very striking. Both have the humeral cross-vein, the distal dichotomy, and an oblique vein towards the distal end of the costal space. Only in *Belmontia* there is an extra veinlet not present in *Rhyacophila*, and the subcosta of the latter extends to

about three-fifths of the length of the wing, as against one-half in *Belmontia*. This difference could easily be removed in the course of evolution, either by actual growth of Sc , or by a reduction in the length of the apical portion of the wing.

In spite of the extra veins present in the radial area of *Belmontia*, the resemblance of this part of the wing to that of *Rhyacophila* is very striking. In both, R_1 is connected with Sc_2 above, and with R_2 below, by cross-veins in closely similar positions. The form and manner of origin of R_{2+3} is practically the same in both; but *Belmontia* possesses an extra vein, R_{3b} , which has been completely eliminated from *Rhyacophila* and all other Trichoptera. The common stalk R_{4+5} is exceptionally short in *Belmontia*. But the tendency of such stalks throughout the whole of the Orders Trichoptera and Lepidoptera is to lengthen; so that the condition found in *Rhyacophila* is a natural derivative from this, as part of the same process by which the extra branches of R_5 have also been eliminated. Cross-veins are absent from this part of the wing in *Rhyacophila*; but there are many other existing genera of Trichoptera in which the inter-radial cross-vein (*ir*) is present, closing the radial or discoidal cell distally.

In *Belmontia* there are four cross-veins between R , or R_s , and M . One of these lies just above the origin of the arculus, and is absent from *Rhyacophila*. The other three connect R_s or its most posterior branches with M_{1+2} or M_1 . Only the middle of these three (*r-m*) remains in *Rhyacophila*.

The media itself is very similar in *Belmontia* and in *Rhyacophila*, the only difference being the extra distal forking of M_4 in *Belmontia*. The position of the median fork (*mf*), not far from the middle of the wing, and the relative positions of the distal forkings, are much the same in both. In *Belmontia*, as in numerous existing genera of Trichoptera, though not in *Rhyacophila*, the median cell (*mc*) is closed by the inter-median cross-vein (*im*); there is also a cross-vein within this cell itself, and cross-veins connecting M_1 with M_2 , and M_3 with M_4 , respectively, which are absent from all recent Trichoptera.

Of the cross-veins connecting M_4 with Cu , *m-cu* is present in

Rhyacophila, but has moved slightly basad, to take up a more advantageous position at the actual forking of M_{3+4} into M_3 and M_4 . The more distal cross-vein, with its continuation across Cu_{1a} to Cu_{1b} , is missing in *Rhyacophila*, as in all existing Trichoptera.

The general scheme of the cubitus is the same in *Belmontia* and in *Rhyacophila*. The cubital fork (*cuf*) lies at a level slightly basad from the origin of *pa*, and the bent portion of Cu_1 arising from the fork is similar in both. The course of the strong, straight, convex vein Cu_1 beyond its junction with *pa* is the same in both; but the apical fork of this vein is larger in *Rhyacophila* than in *Belmontia*. It is quite clear that a slight movement of the median fork distad, with reduction of the fourth apical fork (between M_3 and M_4), correlated with a slight movement of the secondary cubital fork (*cuf'*) basad, and consequent change in the position of *m-cu*, would account for the changes in this region, and could easily have taken place during the period of time elapsing between the Upper Permian and the first appearance of *Rhyacophila* and its allies.

The intercubital cross-vein (*icu*) is absent from *Rhyacophila*, but present in *Belmontia*; the cubito-anal cross-vein (*cu-a*) is present in both, but has moved much further basad in *Rhyacophila*.

Finally, in *Rhyacophila*, as in all existing Trichoptera, the anal area of the forewing has undergone very high specialisation, the three anal veins having become linked up with one another by loss of the distal ends of 2A and 3A, and incorporation of the cross-veins ia_1 , ia_2 in the complex trifurcate vein that is found universally in this region of the forewing of all true Trichoptera. The condition of the anal area in *Belmontia* is the typical archaic condition, from which it has long been clearly evident that such a type of specialisation must have been originally derived.

Unfortunately the area of the jugal lobe, if such exists, is covered over in the fossil; so that we cannot say definitely whether it was triangular, as in *Rhyacophila*, or rounded and less prominent, as in *Chorista* and allies.

Summing up the above evidence, it is quite clear that there is not a single character in the venation of *Belmontia* which precludes its being accepted as the actual ancestor of *Rhyacophila*, and of the whole Order Trichoptera, as now constituted. I do not wish, however, to claim that this newly discovered genus *Belmontia* is itself the *actual ancestor* of that Order; it is quite sufficient to state that *it is the first known representative of a new Order Paramecoptera from which the Trichoptera are undoubtedly derived*. I do not think that the Trichoptera originated in or near Australia; most certainly the *Rhyacophilidae* themselves did not. That being so, we must think of the Paramecoptera either as having existed in other parts of the world also, in Upper Permian times, or as having spread thither from Australia during the Lower Trias. It would then be from some more specialised and reduced type, within the Order, that the true Trichoptera must have been actually derived.

(ii.) *Affinity with the Lepidoptera.*

Let us now turn our attention to the Lepidoptera Homoneura, and compare *Belmontia* with one of the *Micropterygidae*. For this purpose, I shall figure the *pupal wing-tracheation* as well as the *imaginal venation* of the forewing of the genus *Eriocrania*. (Owing to the reduction of the pupal wing-tracheation in all Trichoptera, this comparison could not be made in the case of *Rhyacophila*). This shows that the condition of the cubitus and anal veins, together with the position of the arculus, is closely similar in this pupal wing and in the fossil. In the region of M_1 , of course, *Eriocrania*, like all other Lepidoptera, lacks a separate M_2 , and is thus more highly reduced than *Rhyacophila*. The loss of one of the four usual branches of Rs is peculiar to *Eriocrania*; the missing branch is present in its ally *Mnemonica*, as well as in *Sabatinca* and *Micropteryx*. The forking of Sc into Sc_1 and Sc_2 is retained in *Sabatinca*, *Micropteryx*, and *Mnemonica*, while R_1 also is forked in the first and last of these three genera. The radial cell is closed distally by the cross-vein *ir* in *Sabatinca* and *Micropteryx*, and the primitive dichotomic branching of Rs is preserved in both these genera. In the other genera of the

that the forking of R_1 could have been secondarily acquired, in those genera that possess it, either by splitting of the tip into two (as in *Planipennia*) or by a veinlet taking on the character of a branch vein during evolution of the pterostigmatic region. The fact that the hindwing has a simple R_1 in all genera of the family, might be held to support this; but I think the question is not of sufficient importance to warrant any prolonged argument. If we agree to overlook it, then we may say that *Belmontia* is the first known representative of a new Order from which the *Micropterygidae*, and likewise all other existing *Lepidoptera*, are undoubtedly derived. Bearing in mind the present distribution of the *Lepidoptera* *Homoneura*, it seems quite likely that they did originate somewhere in the Southern Hemisphere; and the fact that Australia is the headquarters for the *Heptaliidae*, while New Zealand is the head-quarters of the *Micropterygidae*, might suggest that this place of origin was not far removed from Australia. That being so, there is, perhaps, a greater chance of *Belmontia* itself having been actually in the ancestral line of the *Lepidoptera* than in that of the *Trichoptera*. The point of importance, however, is that the *Lepidoptera* must in any case have been derived from some type intermediate between *Belmontia* and the *Homoneura*.

We may, then, legitimately claim that both the *Trichoptera* and the *Lepidoptera* are directly descended from the *Paramecoptera*. The archetypes of the *Trichoptera* and the *Lepidoptera*, as at present constituted, contain certain archaic characters not shared by both. For instance, in the *Trichoptera*, there is the retention of M_4 in the forewing, and the non-development of scales; in the *Lepidoptera*, the abdominal prolegs of the larva, the retention of the complete pupal tracheation of the wing, the presence of a frenulum in the hindwing, the small but functional mandibles, and the normal maxillæ (*Micropterygidae*). It is quite clear, therefore, that neither of these Orders can be derived from the other, as Handlirsch plainly showed some years ago (2, p.1253). Handlirsch, however, derived them both from the older *Mecoptera*. We are now able to correct that statement, and to say that the *Trichoptera* and *Lepidoptera* were undoubtedly derived

from a common ancestor which was itself derived from the *Paramecoptera*. It is quite clear, of course, that if we had the whole fossil record before us, we could not say definitely where the *Paramecoptera* ended and the *Trichoptera* and *Lepidoptera* began. It is also quite clear that *Belmontia* itself could undergo considerable further reduction, and still be legitimately regarded as the true ancestral type from which both these Orders have been derived. Our chief satisfaction in the discovery of the new fossil should be, I think, that we have found a type far enough back in point of evolution, as well as in point of time, to indicate not only the true line of descent of these two Orders, but also their true relationship with the much older Order *Mecoptera* and its other near allies.

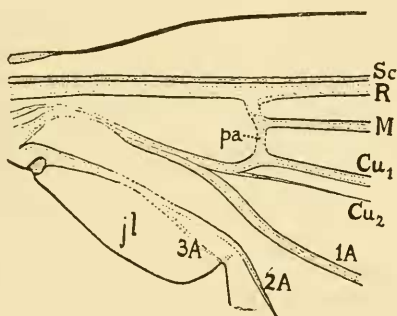
(iii.) *Affinity with the Paratrachoptera.*

We may now turn from the consideration of the *Lepidoptera*, and examine the relationship of *Belmontia* with the group of *Trichopterous*-like fossil insects which I have termed *Paratrachoptera*(7), from the Upper Trias of Ipswich. We do not know the condition of the arculus in any of the four known genera of this Order, the basal part of the wing being not clearly enough preserved for this purpose, even in the beautiful wing of *Aristopsyche*. The vein that I have called Cu_1 in that genus appears to come off directly from near the base of M. Hence it is either the true Cu_1 , attached to M as in most *Mecoptera*; or it may be attached by means of a very specialised arculus, whose junction with the true basal piece of Cu_1 is not clearly visible in the fossil; or it may even be not Cu_1 at all, but the vein M_s complete, before its fusion with Cu_1 is accomplished. Until a more perfect representative of this Order is forthcoming, it is useless to argue as to whether the *Paratrachoptera* can be derived from the *Paramecoptera*. But we should note that *Aristopsyche* has the remains of a true costal vein, separate from the costal border of the wing, and that it has more veinlets in the costal space than are to be found in the same area of *Belmontia*. In these characters, *Aristopsyche* is more archaic than *Belmontia*; while in the lack of the distal forking of the supposed Cu_1 , it is less so.

On the whole, then, we are unable to establish a direct connection between *Belmontia* and the Triassic Paratrachoptera. The latter may possibly be derived rather from the Protomecoptera, which, though only so far known from the Ipswich Trias, must certainly also have existed in the Permian.

(iv.) *Affinity with the Diptera.*

Concerning the areculus in the Diptera, Comstock (1, p.358) has remarked that "owing to the reduced condition of the tracheation in this Order, the elements that enter into its formation cannot be definitely determined." Nevertheless, it seems to me that the condition of this part of the wing in the *Stratiomyidae* (Text-fig.6), as well as in some archaic genera of other families, points definitely to the conclusion that it is formed on the same plan as in the Trichoptera and Lepidoptera.



Text-fig.6.*

The close affinity of the Diptera with the Trichoptera in many other respects is generally recognised, and there can be little doubt also of the close general resemblance of the venational schemes in the two Orders. It is, however, necessary to point out that the usually accepted limits of Cu in this Order are incorrect. The vein usually designated Cu₁ is undoubtedly M₁; this can be proved by reference to the trichiation in the genus *Rhyphus*, as I have already pointed out in a previous paper (5, p.642, note), and by the fact that it actually comes off from the median cell itself in some archaic genera of *Tipulidae*, such as the Australian *Gynoplistia*. Consequently, the true Cu₁ is a strong, usually straight, convex vein, without any distal forking, and the part usually labelled Cu₂ is really the distal continuation

* Basal portion of wing of an undetermined Stratiomyid fly, ($\times 18$). Hornsby, N.S.W.: recent. For lettering, see Text-fig.2, p.238.

of Cu_1 itself. The true Cu_2 arises, as always, close to the base of the wing, but is either a very weakly formed vein (as in Text-fig.6) or entirely lost

Thus we see that, although the Diptera may well be directly derived from the Paramecoptera, as regards their arculus-formation and most other points in their venation, yet we have to explain how it is that they have Cu_1 unbranched, as in the Mecoptera. Either they originally had this vein distally forked, which does not seem likely; or they are descended, not from the Paramecoptera, but from one of the Orders in which Cu_1 is simple, viz., the Mecoptera or the Paratrachoptera.

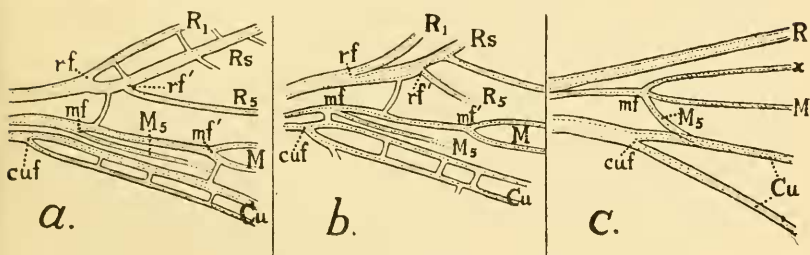
We are bound, then, to conclude that the descent of the Diptera from the Paramecoptera cannot be proved with certainty. That there is a close affinity of some kind between the two Orders appears certain; but the probability is that it is not a directly ancestral one.

(v.) *Affinities with the Megaloptera and Planipennia.*

A remarkable feature in the wing of *Belmontia* is the position of the fork of R_{4+5} , quite close up to the first forking of Rs into R_{2+3} and R_{4+5} respectively. Now Comstock (1, pp.95, 147) has shown very convincingly how the pectinate type of branching found in the Megaloptera and Planipennia can be simply derived from the older dichotomic type, by the recession of the origin of R_4 from its original position on R_{4+5} across to R_{2+3} . The condition shown in *Belmontia* is intermediate between what are usually regarded as the typical dichotomic and pectinate types of branching; i.e., though definitely dichotomic, the origin of R_4 is so close to R_{2+3} that a very little change would produce the pectinate type. Thus we see that, on this character, *Belmontia* could well be the ancestor of both the Megaloptera and the Planipennia.

But, in order to establish this suggestion on a much firmer basis, we must ask for evidence of the presence of the arculus in the two Orders in question. For, if they do not possess this distinctive venational structure, they cannot certainly be descended from the Paramecoptera. Now, in a previous paper (7),

I pointed out a peculiarity in the structure of the media of the Triassic Prohemerobiid *Archepsychops* (Order Planipennia). In this fossil, it is possible to make out a weak posterior branch of M arising quite close to the base, and running parallel to and between M_{1-4} and Cu_1 almost up to the first dichotomy of M_{1-4} . This vein can also be seen in some recent *Psychopsidae*, as may be seen from Text-fig.7, *a*, *b*. I also figure an interesting formation from the hindwing of the archaic Megalopteron *Archichauliodes* (Text-fig.7, *c*). Provided that we are agreed that the areculus is really M_5 , then it is clear that it is the homologue of the vein shown in Text-fig.7. Only, in the *Prohemerobiidae* and *Psychopsidae*, M_5 is in process of degeneration, being crowded out



Text-fig.7.

Portion of base of wing, to show vestige of M_5 or posterior arculus in the Orders Planipennia and Megaloptera. (*a*) forewing of *Megapsychops illidgei* (Frogg.); (*b*) forewing of *Psychopsis elegans* (Guér.); (*c*) hindwing of *Archichauliodes guttiferus* (Walk.); *x* specialised elongated cross-vein from M to Rs. (All figures $\times 12$). For rest of lettering, see Text-fig.2, p.238.

between M_{1-4} and Cu_1 ; whereas, in *Archichauliodes*, it has succeeded in taking on a form not at all unlike that found in Paramecoptera, Trichoptera, and Lepidoptera. Whether the condition of M_5 in the *Prohemerobiidae* and *Psychopsidae* is more primitive than that found in *Belmontia*, it is not very easy to determine. But we should note that, in *Psychopsis elegans*, R_5 is frequently found degenerating also, being crowded out between R_4 and M, as in Text-fig.7, *b*. This seems to point clearly enough to the fact that the condition of M_5 , in those few Planipennia in which it still exists, represents the last stage of degradation, and

is due to the crowding out of this vein, during the rapid proliferation of the branches of Rs that took place during the first formation of the Prohemerobiid type of wing-venation.

The family of Planipennia whose venation most closely resembles that of *Belmontia* is certainly the *Sisyridae*, already recognised as one of the most archaic types within the Order. The pupal tracheation of this family has not yet been studied. Until this can be done, we cannot say definitely that the Planipennia are descended from the Paramecoptera; but enough will have already been said to show that there is quite a fair probability of this being so.

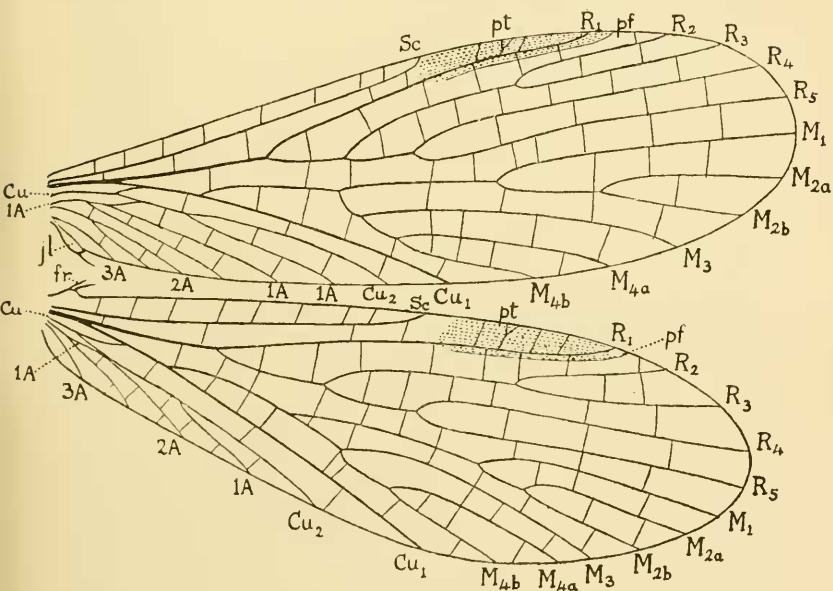
With respect to the Megaloptera, the forewings of this Order either have Cu_1 actually fused with M for a short distance, or the two are connected by what is apparently a cross-vein in the position of the arculus. Both conditions can easily be derived from the more archaic state seen in *Belmontia*, by means of a gradual shortening of the arculus, leading to its final elimination, and the consequent fusion mentioned. We should be careful to remember that, within the single family *Rhyacophilidae* of the Order Trichoptera, all stages may be found from the primitive arrangement, closely resembling that of *Belmontia*, through forms in which *pa* becomes a short, transverse vein, to others in which Cu_1 is actually fused with M. Within this family, the arculus in the genera *Glossosoma*, *Mystrophora*, *Agapetus*, and *Catagapetus* resembles that of *Belmontia* even more closely than it does in *Rhyacophila dorsalis* (Text-fig.4). If, then, all stages from the original type to the most complete reduction can be seen within the limits of a single archaic family, how much more easily may the same series of evolutionary stages be accomplished during the passage from one Order to another?

Thus, though we cannot prove certainly that the Planipennia and Megaloptera are descended from the Paramecoptera, it will be seen that there is quite a fair probability of this being the case. If, when the Belmont Beds have been further worked, no wings of the types associated definitely with these two Orders can be found, then it will become more than ever probable that they did not evolve until later on in geological time; and the

chance that they arose from the older Paramecoptera will become greater still.

(vi.) *Affinities with the Mecoptera and Protomecoptera.*

The affinities of the Paramecoptera with these two Orders are clearly evident; but they are definitely *collateral* relationships, not ancestral. For the Mecoptera already exist alongside the Paramecoptera in the Belmont Beds; while the Triassic Protomecoptera, being more archaic in many respects than the known Mecoptera from Belmont, must also have existed in the Permian, though not yet discovered there.



Text-fig. 8.

Restoration of forewing in the genus *Permochorista* Tillyard ($\times 9$), Order Mecoptera. Upper Permian of Belmont, N.S.W. For lettering, see Text-fig. 2, p. 238.

All three Orders agree in having the original dichotomous branchings of Rs and M_{1-4} preserved. Comparing *Belmontia* with the forewing of *Permochorista* (Text-fig. 8) from the same

Beds, we see the obvious differences of the more complete system of cross-veins in the latter (these were, however, very weakly chitinated), the more symmetrically arched and regularly arranged dichotomies of the veins, the absence of the arculus (as in almost all Mecoptera, owing to the partial fusion of Cu_1 with the main stem of M), and the unbranched condition of the very typically Mecopterous Cu_1 . M_{1-4} is six-branched in the forewing of *Permochorista*, but only five-branched in *Belmontia*, as also in the existing genus *Teniochorista*, which stands very close to *Permochorista* in its general scheme of venation. On the other hand, Rs is only four-branched in *Permochorista*, while in *Belmontia* it is seven-branched.

Thus it is quite clear, apart from the question of *time*, that neither of the two Orders Mecoptera and Paramecoptera can be derived from the other. For the Mecoptera are the older in possessing the more regular dichotomies, the more regular system of cross-veins, the more numerous veinlets in the costal space, and the larger number of branches of M ; whereas the latter have the more archaic type of arculus, the forked Cu_1 , and the larger number of branches of Rs . We must, therefore, postulate, as common ancestor to both Orders, an even more archaic type of Holometabolon, which possessed the archaic features of both.

Turning next to the Protomecoptera, we must compare *Belmontia* with *Archipanorpa* (3, p.188, Pls. viii.-ix.), the only known genus of that Order, from the Upper Trias of Ipswich. The system of cross-veins in this genus is intermediate in completeness between that of the Mecoptera and of *Belmontia*, and the same may be said to be true of the regularity and symmetry of the dichotomous branchings of its veins. *Archipanorpa* is definitely more archaic than *Belmontia* in possessing a well-developed costal vein, distinct from the costal border of the wing, and in having a larger number of branches of Rs and M . It possesses a forked Cu , but the anterior branch Cu_{1a} is partially fused with M_4 ; in this, it is clearly more specialised than *Belmontia*. The region of the arculus is not preserved in either wing of *Archipanorpa*; and hence we cannot complete the comparison.

Thus it is clear again that, apart from the question of *time*,

neither of the two Orders Protomecoptera and Paramecoptera can be derived from the other. A more archaic type of Holometabolon must have existed, somewhere in the Permian, which possessed the archaic characters of both; and this insect would also have possessed the archaic characters of the Mecoptera. In other words, the three Orders Mecoptera, Paramecoptera, and Protomecoptera are to be regarded as being *collaterally related*, all three being separately derived from a single, more primitive, Holometabolous stock. In constituting three separate Orders for these three types, I have followed the wise precedent of Handlirsch in similar cases; since only by this method can the essential differences between them be sufficiently emphasised. Further discoveries at Belmont or Ipswich may perhaps enable us to place all these types definitely within a single enlarged Order Mecoptera, from which all the other Orders within the Panorpid Complex have probably been derived.

We may sum up the evidence as to the affinities of this interesting new fossil Order by saying that it has now been shown to be *definitely ancestral* to the Trichoptera and Lepidoptera, but *of collateral descent* with the Mecoptera and Protomecoptera. It may very possibly be ancestral also to the Megaloptera and Planipennia. With the Paratrachoptera and the Diptera it is not possible, so far, to determine the nature of its affinity, though there is no doubt of a relationship of some kind between them, probably through the Mecoptera. If the only types of Holometabola existing at Belmont be Mecoptera and Paramecoptera, then the probability that all other Orders within the Panorpid Complex are descended from one or other of these two, or from the Protomecoptera of the Trias, would be very great. Thus we leave this interesting problem, in the hope that further discoveries from the Belmont Beds may yet clear the whole matter up, and settle the descent of all these Orders without any doubt.

BIBLIOGRAPHY.

1. COMSTOCK, J. H., 1918.—"The Wings of Insects." Comstock Publishing Co., Ithaca, N. Y., U.S.A.
2. HANDLIRSCH, A., 1908.—"Die Fossilen Insekten, etc." Leipzig.
3. TILLYARD, R. J., 1917—"Mesozoic Insects of Queensland. No. 1. *Planipennia*, *Trichoptera*, and the new Order *Protomecoptera*." These Proceedings, 1917, xlii., Part 1, pp.175-200, Pls. vii.-ix.
4. ————— 1918.—"Permian and Triassic Insects from New South Wales, in the Collection of Mr. John Mitchell." These Proceedings, 1917, xlii., Part 4, pp.720-756.
5. ————— 1918.—"The Panorpid Complex. Part 2. The Wing-Trichiation and its Relationship to the General Scheme of Venation." These Proceedings, 1918, xliii., Part 3, pp.626-657, Pls. lxxvii.-lxxix.
6. ————— 1919.—"On the Morphology and Systematic Position of the Family *Micropterygidae* (sens. lat.). Introduction and Part i. (The Wings)." These Proceedings, 1919, xliv., Part 1, pp.95-136, Pl. iii.
7. ————— 1919.—"Mesozoic Insects of Queensland. No. 5. Mecoptera, the new Order Paratrachoptera, and additions to *Planipennia*." These Proceedings, 1919, xliv., Part 1, pp.194-212.

EXPLANATION OF PLATES XII.-XIII.

Plate xii.

Fig.1.—*Belmontia mitchelli*, n.g. et sp. (Upper Permian of Belmont, N.S.W.). The fossil wing *in situ*, ($\times 8\frac{1}{2}$).

Plate xiii.

Fig.2.—*Belmontia mitchelli*, n.g. et sp. Base of wing, more highly magnified, to show the region of the arculus and the cubital fork, ($\times 19$).

Fig.3.—*Belmontia mitchelli*, n.g. et sp. Arculus and cubital fork still more highly magnified, to show bases of insertion of macrotrichia, ($\times 42\frac{1}{2}$). The arrow points to a clearly marked base of insertion on the arculus itself, while an equally well marked one can be seen on Cu_1 by following the main stem of the arrow backwards. Other similar bases are to be seen on the remaining veins. (The true cross-veins do not carry macrotrichia).

(Fig.1 enlarged from a photograph taken with a triple-extension camera, magnified $\times 4\frac{1}{2}$; Figs.2-3 reproduced from a photomicrograph taken with Reichert's photomicrographic apparatus; Fig.3 an enlargement from the negative of Fig.2).